Responses of the Xylem Anatomy of Species to Environmental Limitations

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Abstract. This study aims to review the main concepts related to the anatomical variation of the secondary xylem and its responses to environmental factors. In this context, this study brings the primary references to anatomical variations of the secondary xylem of species based on comparative approaches in the scientific literature. Classical works on broad floras, such as those by Carlquist [2, 6, 7, 8], Zimmermann [9], Hacke & Sperry [1], and Olson [10], were compared with research on species from the Brazilian Atlantic Forest, such as those by Duarte [5], Cosmo [11,12], Gogosz et al. [13] and Antunes [14]. As a result, it was observed that humid environments tend to select species with wider and less dense vessels, while dry environments favor narrower and more numerous vessels. Changes in these environments due to climate change, which affects water regimes, can make species and ecosystems more vulnerable, especially when not adapted to the new conditions. Therefore, intraspecific xylem variations are important functional indicators to predict impacts at the ecosystem level, identify environmental refugees, and direct forest conservation and restoration strategies. For example, species adapted to waterlogged soil environments can suffer significant impacts when there is a change in the water regime, whether due to artificial drainage, changes in rainfall regimes, or a combination of both. Such species generally have a xylem that is very efficient in conduction but susceptible to cavitation. Finally, secondary xylem analyses can be used to generate vulnerability indicators and predict impacts at the ecosystem level, as well as to promote ecosystem restoration strategies.

Keywords. ecological anatomy, forest ecology, Atlantic Forest, functional wood anatomy, secondary xylem.

1. Introduction

This article analyzes, through a bibliographic review, the study of the anatomical variation of secondary xylem for native trees, mainly from the Brazilian Atlantic Forest, in response to environmental factors to better understand the divergences between environments and species and the importance of further research using the comparative method for climate change.

The xylem structure is closely linked to its function of transporting water by mass flow under negative pressure (the path of water from the roots to the leaf, that is, against gravity). The xylem is formed by dead cells, tracheids and vessel elements, tubular structures with lignified and thick walls, offering rigidity to resist compression [1]. In contrast to the xylem, the phloem conducts sap under positive pressure (leaves to the root) through an active mechanism, a cell that remains alive to maintain the osmotic gradient and protects the system against leaks.

The anatomical adaptation of the secondary xylem is directly related to environmental conditions and is understood through functional ecology and anatomical description. Carlquist [2, 3] developed his comparative anatomy studies for mesomorphic and xeromorphic areas of plants, while in Brazil, there is growing interest in studies focused on hydromorphic environments due to its large territorial extension of environments subject to temporary or permanent flooding. Despite their important role in maintaining water resources and nature conservation, Alluvial forests are still relatively little studied, especially in the Atlantic Forest, where they have low resilience [4,5].

This scenario becomes even more alarming due to climate change, indicating the presence of extreme weather events, such as excessive droughts or heavy

rains, thus affecting the hydrological pattern in alluvial forests. As Duarte [5] discusses, with the increase in the intensity and volume of rainfall, flooding tends to be amplified spatially or temporally in floodplain forests, changing the entire dynamics of species in these environments.

Given this importance, it is essential to understand the ecological significance of variation in vessel characteristics among plants. Such understanding has proven challenging due to the structural, phenological, and habitat effects on vessel characteristics, mainly due to climate change [1].

The next section intends to conduct a methodological explanation to establish the literature review related to the link between anatomical structure and ecological adaptation. It will then address the articles' results and discussions, as well as this paper's conclusion.

2. Methodology

Methodologically, this is a bibliographic review that supports the experiments carried out in the scientific initiation project "Functional Anatomy of the Secondary Xylem of *Citronella gongonha and C. paniculata* (Cardiopteridaceae)" by the project Functional Ecology of Native Plants of the Department of Forestry Engineering of the Federal University of Paraná (UFPR).

The database comes from national and international research with anatomical description of the secondary xylem of the species using the comparative method of wood anatomy. Among the main works carried out outside Brazil, classic authors such as Carlquist [2, 6, 7, 8], Zimmermann [9], Hacke & Sperry [1], and Olson [10] stand out. In Brazil, authors such as Duarte [5], Cosmo [11,12], Gogosz et al. [13], and Antunes [14] were used to discuss species from the Atlantic Forest.

3. Results and Discussions

The responses regarding secondary xylem are intrinsically related to the environment in which the species are found, reinforcing the link between anatomical structure and ecological adaptation. The results and the discussions proposed here focus on establishing these relationships and how climate change impacts the continued preservation of specialist species.

Regarding the anatomical structure of the xylem, the difference between species is based on three main anatomical characteristics: vessel diameter, wall thickness, and structure of intervascular pits. On the other hand, ecological adaptations concern variations in water availability, that is, the difference between drier and wetter environments, that is, species with xerophytic and hydrophilic configurations, respectively. Furthermore, components such as altitude and longitude also alter this conception.

Before delving into the concepts presented, it is necessary to understand the concept of embolism (blockage of vessels by air bubbles). This concept is one of the most important for judging the evolution of secondary xylem and establishing a relationship between vessel diameter and the environment. Resistance to embolism (blockage by air) is defined as the water potential (in MPa) at which there is a 50% loss of conductivity due to embolism [15]. For vessel resistance, we use $(t/b)^2$, which is the square of the vessel wall thickness (t) divided by the conduit diameter (b). This parameter is relevant for determining the resistance to vessel implosion [16], which represents a danger to plants since xylem sap is transported under negative pressure (= tension).

3.1 Evolution and ecological adaptations

The evolution of xylem physiology is complex because, since the early evolution of land plants, xylem has simultaneously performed multiple functions. These include water transport, mechanical support of the plant, and storage of water, minerals, and carbohydrates. In short, the evolution of components occurs by optimizing water transport and promoting resistance to embolisms (blockages by air bubbles), especially in adverse environmental contexts [17].

The process began with simple tracheids, specific to conifers, which were limited in conduction efficiency but offered high protection against embolisms. In the evolutionary process, angiosperms became predominant due to their functional advancement through vessel elements and wider and shorter structures that allowed greater hydraulic efficiency. However, they became more susceptible to embolisms, especially under water stress or freezing. These selective pressures range from climate change, access to light, the species' need for rapid growth, and the ecological complexity of habitats [17].

Carlquist [8] corroborates this concept, arguing that long-term evolutionary trends and more localized ecological adaptations are evident in the secondary xylem. Still, in Carlquist's work, Olson [10] reflects that xylem physiology experiments attempt to connect intraspecific anatomical variations of the xylem to indices of physiological performance, attempting to assess the suitability of species to certain types of environments.

3.2 Relationship between vessel diameter and environment

Carlquist [7] discusses the hypothesis of the relationship between vulnerability to drought-induced embolism and the diameter of the conducting elements; that is, wider conducting elements are more vulnerable than narrow conducting elements due to the more significant

stresses associated with drought. Finally, their research concludes that plants in dry and cold environments, on average, have narrower vessels than plants in hot and humid environments [2, 3, 18, 19].

Thus, wider and less frequent vessels have greater efficiency but less protection against cavitation. On the other hand, narrower vessels (commonly in xerophytic climates), more numerous and more grouped, have lower conduction efficiency but more excellent protection against cavitation. These patterns of variation occur in response to contrasting conditions. They can be observed both in comparisons between different species [13] and between individuals of the same species (intraspecific variation) [12].

With these concepts in mind, most studies are focused on the relationship between vessels and dry climate, so it is necessary to apply this scenario to the Brazilian Atlantic Forest.

Atlantic Forest species generally have xylem vessels with large diameters and low density, a typical pattern of species that live in humid environments (tropical and subtropical hygrophilous). Cosmo et al. (2012) report that Tapirira (*Tapirira guianensis* Aubl.) has anatomical characteristics similar to *Vitex megapotamica* (Spreng.) Moldenke, *Luehea divaricata* Mart., *Didymopanax morototoni* (Aubl.) Decne. & Planch. and *Gymnanthes klotzschiana*. Also, Cosmo et al. [12] states that specialist hydrophilic species, even more adapted to water, such as *Calophyllum brasiliense* Cambess., *Erythrina crista-galli* L. and *Tabebuia cassinoides* (Lam.) DC., have even wider vessels and lower densities compared to xerophytic and mesophytic species.

3.3 Climate change and impact on functional ecology

Regarding climate change, in tropical environments, the amount and seasonality of precipitation have a decisive influence on the structure and productivity of the forest [20]. Changes in rainfall patterns and soil moisture cause more severe and widespread drought conditions, reducing underground availability and impacting species' survival [21]. Tropical species (mostly angiosperms) are suffering from increasing water stress and operate within a narrow hydraulic safety margin [20], being very susceptible to embolism [13]. Such factors make species increasingly vulnerable concerning their survival and distribution, clearly threatened by drought [21].

Several studies use xylem characteristics as indicators of vulnerability [21, 14, 22, 23, 24, 25, 26] and such parameters become useful for predicting impacts at the ecosystem level (large scale) [22]. Therefore, interspecific variation (between species) becomes valuable in establishing adaptation strategies, species conservation, detecting and protecting "hydrological refuges," and understanding and extending the effects of climate change. Knowing species sensitivity is necessary to predict ecosystem responses to future conditions [27].

These extreme climate variations do not only refer to extreme drought events but also to flooding, whether permanent or temporary [28]. The differences in water availability can cause intraspecific variation through genetic (ecotypic) differentiation and/or phenotypic plasticity [20]. This intraspecific variation demonstrates vulnerability to drought-induced embolism in response to changes in water availability in some species [29,30]. All these parameters are essential for managing ecosystems under the most diverse conditions and identifying valuable species for ecosystem restoration projects [31].

The most flood-tolerant tree species significantly influence the structure and functioning of hydrophilic forests, with the dynamics being determined by the species' plasticity [31]. Despite the high-water conduction, changes in the hydrological regime of soils can lead to significant changes at the ecosystem level. One of the ecosystems at risk is the Histosols, which are prone to degradation when drained [31,32].

4. Conclusion

Variations in xylem among species from dry, humid, and hydromorphic environments impact the distribution of woody species. Changes in water conditions can, therefore, result in irreversible losses for species and, consequently, for ecosystems.

This also depends on plants' ability to cope with climate change, whether in extreme floods or droughts. Limited data on xylem responses across a wide range of climates and ecosystems, such as alluvial environments, make it difficult to generalize response patterns for many species.

It is very important to develop analyses of secondary xylem to generate indicators of vulnerability, predict impacts in many ecosystems that are still little explored, and promote restoration strategies.

5. References

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